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Motivation for the greater good: neural mechanisms of overcoming costs

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Running head: Neural mechanisms of overcoming costs

Motivation for the greater good:

Neural mechanisms of overcoming costs

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Abstract

To obtain greater goods decision makers often have to incur and endure costs. Here we review mechanisms that enhance the willingness to accept and overcome costs in individual and social settings. General, cost-invariant mechanisms involve controlling and reducing reward-related impulsivity, abstracting from personal and situational circumstances, changing the availability of options in the choice set, and reinterpreting aspects of the choice alternatives. These mechanisms are based on fronto-striatal and fronto-parietal networks for valuation and goal-setting. More specific, cost-variant mechanisms include effort endurance, imagining future events, tolerating risk, and empathy. These mechanisms rely on cost-specific brain mechanisms, as well as interactions with the valuation network in accordance with cost-variant changes in the valuation of the costly choice alternatives. We identify knowledge gaps, which are exacerbated by studies typically focusing only on one cost type. Moreover, many of the identified mechanisms of enduring costs provide largely untrodden paths for interventions to increase cost endurance in clinical and non-clinical domains.

Introduction

Goal directed actions and value-based decision making rely on implementing the course of action or choosing the choice alternative with the best balance between subjective costs and subjective benefits. With typical value-based decisions, the alternatives with greater benefits are also more costly. Accordingly, when decision makers experience a trade-off between high cost, high benefit versus low cost, low benefit alternatives (Table 1), they may follow paths of less resistance and choose alternatives with smaller costs. As the choice of the more costly alternative may be in some sense better for the decision maker or desired by society, the question arises whether and how the willingness to accept costs and the capacity to endure them can be increased so that agents obtain greater goods. Here we address this question with a focus on psychological and neural mechanisms, reviewing mostly human imaging and transcranial stimulation studies. For methodological reasons, these stimulation studies are limited to the cortex and neglect subcortical brain regions, whereas a review of single cell recording and optogenetic stimulation studies would concentrate more on subcortical structures.

Costs come in different forms, such as effort, time, risk, and selfishness. Although the modalities of these costs differ, their subjective value can be measured experimentally with generic currencies such as money in humans or juice in animals. For this review, we propose a classification scheme that distinguishes cost-invariant (domain-general) from cost-variant (domain-specific) approaches to increasing cost endurance. Cost-invariant mechanisms can be used to tilt the cost-benefit balance in the direction of higher cost, higher benefit alternatives irrespective of the type of costs or to sculpt the choice space such that lower cost, lower benefit alternatives are less likely to be chosen. Cost-variant approaches subjectively modify the properties of specific cost types. For example, practicing a particular type of effort would reduce the perceived cost of exerting this effort but typically not generalize to increased willingness of enduring other types of costs. It should be kept in mind though that the assignment of findings to cost-invariant and cost-variant categories remains somewhat tentative in several cases,

simply because the question has not been investigated yet as studies often look at only one rather than multiple cost types.

At the neural level, cost-invariant routes to tilting the cost-benefit balance in favor of cost endurance for greater goods involve regions that process value irrespective of outcome type such as the striatum and the ventromedial prefrontal cortex (VMPFC). We consider also mechanisms that reduce reward-related impulsivity, i.e., the temptation to give in to selecting low cost, low benefit alternatives, implemented by dorsolateral prefrontal cortex (DLPFC); mechanisms that facilitate viewing costly choice alternatives from a more distanced perspective, implemented by the temporoparietal junction (TPJ); and mechanisms involved in removing lower cost, lower benefit alternatives from, or adding higher benefit alternatives to, the set of available alternatives, underpinned by the frontal pole (FPC) (Figure 1). Moreover, it appears that cost-variant endurance regions can modulate the regions involved in cost-invariant endurance mechanisms (Figure 2).

Cost invariant mechanisms

Cost invariant mechanisms serve general functions for goal-directed behavior, such as context-sensitive precision of choice or mental simulation and search [1]. Accordingly, although we focus in the following on how these mechanisms can facilitate the choice of high cost, high benefit alternatives, it is worth noting that they can just as well facilitate the choice of low cost, low benefit alternatives in situations where high cost, high benefit alternatives are tempting but ultimately have lower subjective value. In line with this view, brain regions underpinning cost-invariant mechanisms also are sensitive to choice difficulty (e.g., [2,3]). Such activity may reflect exertion of cognitive control, which during cost-benefit decisions may reflect the (context-sensitive) goal of increasing choice precision according to subjective value.

Reducing reward-related impulsivity

Impulsivity can relate to the motor domain (response disinhibition) or to the reward domain, with distinct neural underpinning [4]. Here we focus on reward-related impulsivity, where tempting but ultimately less beneficial alternatives are chosen. Reward-related impulsivity is particularly well-characterized in the domain of delay costs, when immediate smaller rewards are preferred over waiting for larger-later rewards. Accordingly, controlling or reducing reward-related impulsivity reduces the tendency to select immediate rewards and thereby promotes patience for larger rewards in the future [5,6]. Neurally, this mechanism is implemented by a corticostriatal network in which DLPFC top-down modulates neural value signals in striatum and VMPFC [7,8] (Figure 1), thereby enhancing neural value representations of delayed relative to immediate rewards.

A similar mechanism is hypothesized to inhibit also selfish impulses in social interactions [9]. Studies agree on a role of DLPFC activity for social impulse control but disagree on whether the impulse being controlled is for prosocial [9,10] or selfish [11,12] behavior. In keeping with the cost-invariant nature of impulse control, its function for social decisions can be flexibly adapted to internal (e.g., antisocial personality disorder [9,13], individual differences in socio-economic status or prosociality [12,14]) and external (e.g., threat of punishment [11]) contexts. By extension, the target of impulse control may depend on which choice option is associated with an impulse (selfishness or costly sharing in the social domain).

Impulse control deficits and prefrontal dysfunctions may also contribute to the excessive risk-taking behavior that is observed in several psychiatric disorders [15-17]. In line with this conjecture, brain stimulation targeting DLPFC was reported to reduce reward-related impulsivity in risky decision-making [18,19], suggesting that the costs of risk-seeking behavior can be overcome by promoting reward-related impulse control.

While reducing reward-related impulsivity allows overcoming various types of costs, it is important to note that exerting reward-related impulse control requires (mental) effort and is

therefore experienced as costly itself [20,21]. Reward-related impulse control thus plays a two-sided role in trading off costs against benefits, because an individual has to weigh whether a goal (for example, a larger-later reward) is worth exerting reward-related impulse control. Notably, this account predicts that individuals will decide to exert reward-related impulse control only if the subjective net benefit expected from choosing the high cost option and exerting reward-related impulse control exceeds that of the control-free, low cost, low benefit option [20].

Distancing

A tried and tested cost-invariant method of increasing cost endurance is for decision makers to distance themselves from their current situation [22,23]. By projecting themselves mentally into the future, into a more remote spatial location, or into the mind of somebody else, decision makers appear to be less exposed to their current emotions and better able to overcome costs. Recent evidence suggests that the tendency to devalue delayed reward and reward received by more distant others is processed by common brain regions [24] and counteracted by the ability for perspective taking [25]. Specifically, activity in the TPJ appears to facilitate both overcoming present bias in mental time travel [26] and egocentricity bias in social interactions [27,28]. Accordingly, disrupting TPJ function with continuous theta burst (cTBS) transcranial magnetic stimulation (TMS) reduces the willingness to wait and be generous, i.e. to overcome temporal and selfish costs [25], in line with the notion that the TPJ facilitates cost-invariant cost endurance through distancing (Figure 1). For the social domain, the TPJ was shown to facilitate prosocial behavior by increasing the value of sharing in value-encoding regions of VMPFC [27].

Changing the availability of choice options (option editing)

In well-structured choice situations where one course of action has to be taken, the high cost, high benefit outcome can be secured by removing the low cost, low benefit option from the space of available alternatives [29-31]. In other words, through precommitment, people can restrict exposure to tempting but ultimately worse options and thereby insure themselves against failures in reward-related impulse control. At the neural level, the FPC is more active during binding than non-binding choices of larger later rewards (Figure 1) and communicates with regions involved in the control of reward-related impulses, such as the DLPFC and posterior parietal cortex at the time of precommitment decisions [32]. Moreover, upregulation of frontopolar activity with anodal transcranial direct current stimulation (TDCS) increases the number of precommitment decisions without affecting other cost-invariant functions such as preference for larger rewards or reward-related impulse control [33]. Thus, FPC appears to play a crucial role for restricting the choice space through precommitment.

The opposite of precommitment is to generate further choice alternatives. This function is particularly important in ill-structured real-life situations and impaired in patients with reduced motivation [34]. Moreover, by creating additional courses of action, one may be able to reach a given goal without having to endure as many costs as with the given alternatives. Interestingly, the FPC is also more active during option generation than during a control condition where options are read passively [35]. Taken together, precommitment and option generation data point to a central role of FPC in sculpting the choice space for goal-directed actions and value-based decisions.

How exactly the FPC implements the sculpting of the choice space is not entirely clear yet. While the FPC has been associated with several functions, probably the most relevant in the current context is its proposed role in processing the values of alternative (typically unchosen) choice options [36]. In line with this function, enhancing FPC excitability with anodal tDCS increases the willingness to exert both mental and physical effort for rewards [37].

In other words, typically rejected high cost, high benefit options became more valuable under stimulation, speaking to one possible mechanism with which FPC may sculpt choice space.

Framing

The way choice options are presented crucially determines how the values of these options are processed, a phenomenon referred to as “framing”. Accordingly, overcoming various types of costs can be facilitated by framing choices such that a higher value is assigned to the high cost, high benefit relative to the low cost, low benefit option. Evidence for framing effects originally stems from the domain of risky decisions, where humans are risk-seeking if outcomes are framed as losses but risk-averse if outcomes are framed as gains [38]. Thus, while for gains variability (as compared to safe lower rewards) is perceived as cost, in the loss domain individuals experience highly likely or safe losses (relative to less likely higher losses) as subjectively more costly. This allows to bias an intended behavior by framing a choice problem accordingly: if risky behavior is more costly in a given context (e.g., smoking, obesity, unprotected sex), the outcomes should be presented as gains to bias risk-averse actions.

The effectiveness of re-framing choice problems for biasing desired outcomes is not restricted to the domain of risk, as framing was also found to promote patience in intertemporal decisions [39,40] and to modulate social preferences [41]. On a neural level, framing generally appears to modulate activation in brain regions that are related to the processing of the subjective value of costs and rewards, such as insula, amygdala, and VMPFC [40,42,43]. Moreover, framing can reduce reward-related activity in the striatum [39,40] (Figure 1).

Cost variant mechanisms

Enduring more mental and physical effort

In everyday life, obtaining larger rewards often requires exerting more mental or physical effort (subjective strain) than obtaining smaller rewards. Accordingly, effort-based

decisions consist of a trade-off between high effort, high reward versus low effort, low reward options (Table 1). By extension, one method of overcoming high effort costs in a cost-variant fashion consists of reducing the subjective strain of exerting high effort.

The subjective costs of exerting mental effort are thought to be encoded in lateral prefrontal cortex [44,45] and amygdala [46], whereas the costs of physical effort have been associated with the supplementary motor area (SMA) [45,47,48]. Note though that common coding of both cost types may be more prevalent than cost type-specific coding, and has been reported in dorsal anterior cingulate cortex (ACC), DLPFC, intraparietal sulcus, and insula [46]. Mental or physical training facilitates performance in the trained types of effort and modulates activation in brain regions related to effort production [49,50]. However, these regions relate not only to the goal-directed production of effort, but they are also hypothesized to encode the expected effort costs when deciding whether or not to engage in effort (before the actual effort production). If this hypothesis is correct, it should be possible to enhance the willingness to exert effort by suppressing or disrupting neural activity in these regions. Indeed, a recent study reported that disrupting the SMA with cTBS-TMS increased the motivation to engage in rewarded physical effort by lowering the perceived strain of effort in a grip force task [51] (Figure 2A). Neural interventions targeting the neural basis of subjective effort demands therefore allow improving the motivation to overcome effort costs.

The motivation to engage in rewarded effort may depend not only on the expected benefits and the required costs per se, but also on how an individual weighs effort costs against the rewards at stake. The ACC is thought to play a central role in trading-off effort costs against benefits [20,52], given that ACC is structurally and functionally connected to the ventral striatum [53] as well as to regions encoding cognitive and physical effort costs, such as the SMA [47,54]. The ACC has therefore been hypothesized to motivate effortful behavior by top-down modulating striatal value signals [55]. In fact, ACC lesions reduce the willingness to exert both physical and mental effort for rewards [56,57]. The ACC may thus integrate information

on the incentive value of rewards at stake and the required effort costs in order to decide whether a reward is worth the effort.

Finally, it is conceivable that noradrenergic projections to the ACC [58] contribute to these decisions. In any case, decisions that a reward is worth the effort were found to be followed by increased activation of noradrenergic neurons in the locus coeruleus [59,60]. Thus, noradrenaline may have a crucial role for energizing behavior during effort production.

Waiting longer

Temporal delay devalues given benefits (Table 1). Waiting longer for larger benefits rather than selecting smaller sooner benefits requires enduring not only opportunity costs but in some cases also cognitive costs due to the need to delay gratification. One way of increasing the ability to wait in a time cost-variant fashion is to project oneself into the future. For example, reminders of personal events that will happen at a particular time in the future facilitate choice of larger later benefits at those future time points compared to a condition without reminders [61]. The effect of the reminders increases with the vividness with which one imagines the future events. Thus, the ability to imagine future events, including the ability to imagine rewards more generally [62], is associated with increased willingness to endure delay costs. An obvious follow-on question is whether imagination of future events can be trained and whether such training facilitates waiting longer. Research in elderly participants [63] and in the motor domain [64] suggests that such interventions can result at least in changed imagery and brain responses.

At the neural level, imagination is associated with activity in VMPFC and lateral parietal cortex and the individual size of the behavioral imagination effect correlates with activity in a subregion of the ACC [61,65]. Gradations in coupling of this ACC region with the hippocampus (and the amygdala) underlie gradations in the size of the imagination effect particularly for unfamiliar future events whereas familiar future events rely more on ACC-ventral striatum coupling [66] (Figure 2B). Thus, distinct properties of the imagined future events appear to be

reflected in distinct neural interactions, even though the facilitating effects on patience are similar. Moreover, the findings are in line with recent literature showing that frontostriatal connectivity facilitates patience [67-70], although it remains unclear how specific this connection is to enduring temporal as opposed to other types of costs.

Taking more risk

For gains, humans are typically risk averse; in other words, up to some point, they prefer safer alternatives over riskier alternatives even if the returns (expected values) of the safer alternatives are lower than those of the riskier alternatives (Table 1). Viewed from this perspective, risk is a cost in the gain domain and may or may not be overcome by appropriate circumstances, task designs, or interventions. One possibility arises from (perceived) stake size. Compared to large stakes, small stakes are also associated with less risk aversion (or even risk-seeking rather than risk aversion [71]). Moreover, poverty, risk of starvation and externally set targets all are thought to increase risk taking, particularly of course if the amount provided by safe alternatives is not sufficient for survival or for reaching the targets [72,73]. It should be kept in mind though that once critical wealth thresholds surpassed, risk aversion increases [74,75]. In-line with this mechanism of counteracting risk costs, reward regions such as the striatum and VMPFC keep track of current wealth and the context in which gains occur, both within tasks [76,77] and individuals [78]. A model that assigns the influence of current wealth level to decision bias rather than subjective value representation best explains how wealth affects the propensity to make risky decisions [77]. Moreover, increasing pressure to make risky decisions because targets are not yet attained appears to be tracked by dorsomedial prefrontal cortex [79].

Stimulation studies suggest that interventions targeting DLPFC affect risk taking, although the degree to which these interventions are cost-variant remains to be investigated. For example, disrupting right DLPFC function with 1-Hz repetitive TMS increases risk taking

[80], whereas anodal tDCS of right DLPFC reduces it [81] (Figure 2C). Under a cost-invariant reward-related impulse control interpretation of these results, DLPFC would control the impulse elicited by the lure of large gains. However, the effects of DLPFC stimulation on risk taking seem to be more pronounced in ‘cold’ tasks, where the outcomes of risky decisions are not realized in every trial, than in ‘hot’ tasks, where participants experience outcomes after each decision ([82]; see also [83]). This finding suggests that reward-related impulse control may not be the mechanism through which DLPFC contributes to risk aversion, at least under the assumption that reward-related impulses are stronger in hot than cold tasks.

Another stimulation study proposes a rather specific effect on risk taking of parietal cortex. Specifically, downregulation of left intraparietal sulcus (IPS) with 1-Hz repetitive TMS increases risk aversion for gambles with high variance ($p=0.5$), without affecting ambiguity aversion or risk preferences for gambles with lower variance ($p=0.25$, $p=0.75$). However, the high variance gambles also happened to be closest to indifference in the control stimulation condition, which could have facilitated finding a TMS-effect [84]. By extension, one may want to test whether upregulation of IPS would facilitate risk taking.

Helping others

Sharing goods with others is costly if the act of giving reduces one’s own outcome. However, sharing is also considered as highly desirable in most societies. Accordingly, trade-offs can arise between maximizing one’s own outcome and costly helping others, raising the question of how the selfish impulse of avoiding costs to oneself can be overcome in order to create higher social benefits. One important motivation for costly sharing is empathy, the capacity to feel what another person is feeling. Empathic concern for others’ suffering appears to be a driving force for altruistic behavior [85-87]. Empathy for the outcomes of others may also be fueled by a preference for equality [88], a further mechanism for overcoming selfishness [89].

At the neural level, empathy for the pain of others has been related to activation in anterior insula [85,90] (Figure 2D). Moreover, connectivity of the anterior insula with the anterior cingulate cortex predicts helping behavior [91]. The link between empathy and costly helping is further evidenced by findings that empathy can activate regions of the dopaminergic reward system [86], which encodes not only selfish outcomes but rewards for others as well [92-94]. Recent evidence suggests, however, that the dopaminergic system's sensitivity to costly sharing may be gender-specific, with the dopaminergic system being more sensitive to shared than selfish rewards in women and to selfish than shared rewards in men [95]. Thus, in females, the dopaminergic system might underpin the experience of a “warm glow” promoting costly giving.

Discussion and conclusions

We proposed a systematic classification scheme of cost-invariant and cost-variant mechanisms for overcoming various types of costs in value-based decision-making. Cost invariant mechanisms modify how decision makers respond to (reward-related impulse control) or perceive (distancing, framing) the properties of choice options or of the choice set (option editing). These mechanisms are involved in overcoming more than one type of cost and are thus more powerful than cost-variant mechanisms, which modify the cost-specific aspects of outcome and action representations.

At the neural level, the distinct mechanisms for overcoming costs are implemented by dissociable brain regions. DLPFC implements control processes that inhibit the impulse to choose less costly, but also less beneficial options across various domains of cost types, consistent with a general function of DLPFC for cognitive control and goal-directed behavior [96,97]. Also other brain regions related to cost-invariant and cost-variant mechanisms, such as FPC and ACC, are well known to contribute to successfully pursuing one's goals [20,98,99]. The TPJ, in contrast, had mainly been linked to social cognition so far, but recent evidence

suggests the TPJ to play a role for overcoming the costs of delayed rewards as well [25]. Most of these mechanisms bias the decision for costly larger rewards by top-down modulating neural value signals encoded in VMPFC and striatum, which are both innervated by dopamine neurons. The dopaminergic value system thus represents a key player for trading off rewards against the required costs, which is supported by findings showing that dopaminergic manipulations change the willingness to overcome costs in all domains discussed here [93,95,100-102].

From a clinical perspective, the multitude of mechanisms that can be invoked to overcome costs may explain why disorders or lesions sometimes have more limited effects than one would expect. Yet, basic motivation to overcome larger costs for larger benefits is a fundamental prerequisite for deploying alternate mechanisms in the first place. Accordingly, disorders that affect this motivation and its neural basis may be most susceptible to showing more profound deficits. Examples include disorders with pronounced negative symptoms, such as depression [103], schizophrenia [104], and Parkinson's disease [105]. In other disorders, cost-benefit calculations change through the repeated (impulsive or compulsive) use of reinforcers, such as addiction and obesity [106]. For all of these disorders, methods that upregulate motivation for attaining behavior change and ultimately clinical improvement may be associated with high costs but eventually higher benefits. Some of the present interventions have already been applied to a clinical context (although interventions often use a non-motivational focus [107,108]). For example, in an option-editing study conducted in Nova Scotia (described in [109]), out of 88 compliant gamblers, 55 reduced overall spending, six showed no change and 27 increased spending with a voluntary pre-commitment device that allowed limiting the amount and time that people could gamble. Likewise, a similar trial in Australia found that spending increased particularly in those gamblers who made no use of the precommitment device of setting a spending limit [109]. The effects of interventions likely depend on how exactly they are implemented, with the possibility of unintended effects. In any

case, we see untapped potential particularly for psychiatric disorders suffering from impairments in overcoming costs. For example, addiction has been conceptualized as reduced ability to delay gratification [110], and interventions mainly targeted impulse control skills and DLPFC to improve resistance to immediate rewards [111]. However, as reward-related impulse control is only one mechanism contributing to delaying gratification, it may be worth exploring the effects of interventions that target distancing or option editing as well. The above reported study on the effectiveness of precommitment devices for pathological gambling suggests that such intervention strategies might improve self-control particularly in impulsive individuals.

It should be noted that the present scheme is limited by the fact that studies typically investigate one cost type and one mechanism at a time. Moreover, even within the mechanisms and cost types considered here, substantial gaps remain in the literature (Table 2). A fruitful approach for future research might thus be to fill these gaps by testing a potential involvement of cost-invariant mechanisms also in domains where the contribution of a particular mechanism has not been clarified yet. Similarly, mechanisms considered as “cost-variant” here might turn out to be involved in overcoming other cost types as well. For example, several studies suggest that the ACC may perform cost-benefit computations in multiple domains, even though this has not been tested fully so far. We therefore consider our schema for cost-variant and –invariant mechanisms to represent merely the current state-of-the-field that will be complemented and modified by future research.

It is further worth noting that the definition of “cost” turned out to be highly context-specific: both risk-proneness and risk-aversion prevent achievement of larger expected values. Likewise, in patients with antisocial personality disorder selfishness represents the costs that need to be overcome, but the opposite – extreme prosociality – might be considered as dysfunctional as well [112]. Here, the function of mechanisms promoting goal achievement like reward-related impulse control is determined by an agent’s goals in a given situation. Thus, individual differences co-determine the definition of what is costly [113].

To sum up, the schema of cost-variant and cost-invariant mechanisms we developed here shows the commonalities, but also the distinctiveness, between neuro-cognitive mechanisms for overcoming costs. A deeper understanding of these mechanisms may allow improving cost-endurance in both healthy individuals and psychiatric populations.

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Tables

Domain	Cost	Trade-off (high cost, high benefit vs. low cost, low benefit)
Effort	Doing mental or physical work	Higher effort, higher value vs. lower effort, lower value
Time	Waiting for delayed outcomes	Later, larger rewards vs. sooner smaller rewards
Risk	Variability in gains (gain frame)	Higher risk, higher expected value vs. lower risk, lower expected value
	Certainty of loss (loss frame)	Sure loss, higher expected value vs. risky loss, lower expected value
Social	Sharing goods with others	Smaller self, larger social rewards vs. larger self, smaller social rewards

Table 1. Overview over cost domains, cost types, and trade-offs in cost-benefit decision-making. Expected value = sum of probability-weighted outcome magnitudes

	Reducing reward-related impulsivity	Distancing	Option editing	Framing
Effort	[20,21]		[34,35]	
Time	[5-8]	[25]	[32,33]	[39,40]
Risk	[18,19]			[38]
Social	[9-12]	[25,27,28]		[41,42]

Table 2. Overview of studies as a function of cost type (rows) and cost-invariant mechanisms (columns) for overcoming costs. Note that studies typically investigate one single cost type together with one single mechanism.

Figure captions

Figure 1. Neural basis of cost-invariant mechanisms. Dorsolateral prefrontal cortex (DLPFC) implements goal-directed behavior by controlling and reducing reward-related impulsivity, whereas temporo-parietal junction (TPJ) allows overcoming egocentricity bias and directing attention to the future or to the needs of others (distancing). DLPFC and TPJ shift the cost-benefit balance towards costly larger rewards by top-down modulating neural value signals in VMPFC and striatum. Frontopolar cortex (FPC) has a general role in evaluating conflicting goals and sculpting choice space (option evaluation/editing) and may implement precommitment decisions via top-down modulating DLPFC. Framing modulates brain activity in regions processing the values of rewards and costs, such as the VMPFC and the striatum.

Figure 2. Neural basis of cost-variant mechanisms. (A) In effort-based decision making, the anterior cingulate cortex (ACC) trades off the expected benefits against the subjective strain of exerting effort. Subjective strain of cognitive and physical effort appears to be encoded by DLPFC and supplementary motor area (SMA), respectively. If the expected benefit is considered worth the effort, locus coeruleus (LC) energizes behavior via noradrenergic projections to ACC. (B) In intertemporal decision-making, the ACC is related to projecting oneself into the future in order to overcome delay costs. Moreover, the ACC shows functional coupling with the hippocampus when imagining unfamiliar future events and with the striatum when imagining familiar future events. (C) Risk aversion is implemented by DLPFC, with the strength of risk aversion depending on an individual's current wealth status which is tracked by striatum and ventromedial prefrontal cortex (VMPFC). (D) In social interactions, empathic concern for others' suffering is encoded by the anterior insula and ACC.

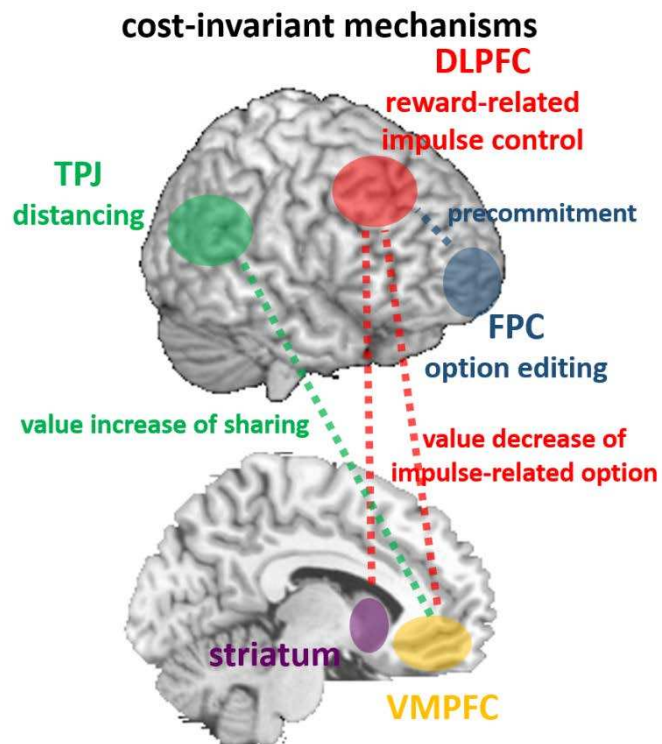
Figure 1

Figure 2

